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Dietary Inferences Through Buccal Microwear Analysis of Middle and Upper Pleistocene Human Fossils

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ABSTRACT Buccal microwear has been studied in a sample of 153 molar teeth from different modern hunter-gatherer, pastoralist, and agriculturalist groups, with different diets (Inuit, Fueguians, Bushmen, Australian aborigines, Andamanese, Indians from Vancouver, Veddahs, Tasmanians, Lapps, and Hindus), preserved at museum collections. Molds of an area of the buccal surface have been obtained and observed at 100× magnification in a scanning electron microscope (SEM). The length and orientation of each striation have been determined with a semiautomatic program of an image analyzer system (IBAS). Results show that intergroup variability is significantly higher than the intragroup variability. There exists a tendency toward fewer striations and a higher proportion of vertical striations in the carnivorous groups than in the vegetarian ones. This microwear pattern is concordant with biomechanics (predominantly vertical mandible movements in meat eaters) and phytolith content in plants (more abrasive particles in vegetarian diets). The variability found has been used in a multivariate analysis as a base to compare the microwear pattern of a sample of 20 Middle and Upper Pleistocene fossils, mainly from Europe, analyzed with the same methodology. The sample includes specimens usually classified as archaic *H. sapiens* (Broken Hill, Banyoles, Montmaurin, La Chaise-Suard, La Chaise-Bourgeios et Delaunay), Neanderthal (La Quina V, Gibraltar 2, Tabun 1 and 2, Amud 1, Malarnaud, St. Cesaire, Marillac), and anatomically modern *H. sapiens* (Skhül 4, Qafzeh 9, Cro-Magnon 4, Abri-Pataud, Veyrier, La Madelaine, Rond-du-Barry). Results indicate that some of the Neanderthal specimens have a microwear pattern close to that of the carnivorous groups (such as Inuit and Fueguians), suggesting that these individuals follow a hunter strategy. In contrast, archaic *H. sapiens* and *H. sapiens sapiens* seem to have a more abrasive diet, probably more depending on vegetable materials, than the Neanderthals.

Tooth striation analysis, especially for the occlusal surfaces of teeth, has been the focus of extensive work in the literature (Bullington, 1991; Covert and Kay, 1981; Fine and Craig, 1981; Grine, 1984, 1986; Gordon, 1982, 1984a,b, 1988; Gordon and Walker, 1983; Kay, 1987; Kay and Hiiemae, 1974; Maas, 1991; Puech, 1976, 1978, 1979, 1982; Puech and Pant, 1980; Puech et al., 1980, 1983a,b, 1986; Ryan, 1979; Ryan and Johanson, 1989; Teaford, 1985, 1991, 1994; Teaford and Glander, 1991; Teaford and Leakey, 1992; Teaford and Oyen, 1989; Teaford and Robinson, 1989; Teaford and Runestad,

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1992; Teaford and Tylenda, 1991; Teaford and Walker, 1984; Ungar, 1992, 1994a,b; Walker, 1979, 1981, 1984). However, there is still little information about the variability of striation patterns on the buccal surface of teeth (Lalueza and Pérez-Pérez, 1993; Lalueza et al., 1993; Pérez-Pérez et al., 1994). Our studies on the intrapopulation variability of the buccal striation pattern on the postcanine dentition suggest that interpopulation comparisons may yield valuable information about dietary habits from human fossil remains. The buccal microwear pattern seems to be conservative within individuals, independent of the analyzed tooth, and the interindividual variability seems to be significantly larger than the intraindividual variability (Pérez-Pérez et al., 1994). In addition, the buccal striation pattern seems to need a long period of time to be fully attained, and therefore slight seasonal variations in dietary habits may not significantly affect it (Pérez-Pérez et al., 1994). These observations suggest that the analysis of the buccal striation pattern may be successfully applied to the study of the diet of past human populations. Although several studies have analyzed the buccal tooth surface of hominid fossils, such as Mauer, Aragó, Broken Hill, and others from East Africa (Puech, 1978, 1982; Puech et al., 1980, 1983b), most buccal microwear studies to date lack a populational perspective and thus must be viewed cautiously. The approach made by Fine and Craig (1981) aimed in this direction, but the authors themselves considered that more populations and larger samples were needed because they included samples of only two hunter-gatherer populations and one agriculturalist: Eskimos ($n = 6$), Australian Aborigines ($n = 9$), and Hindus ($n = 4$).

The aim of this paper is to analyze the buccal microwear pattern of several populations of hunter-gatherers, pastoralists, and agriculturalists. If the interpopulation variability is significantly larger than the intrapopulation variability, the buccal microwear pattern may be applied to the analysis of human fossil remains. One crucial question that can be controversial is whether the variability observed in modern human populations can be assumed for past populations. This problem arises in one way or another in every field of paleoanthropology. However, if we want to make dietary inferences for fossil remains using microwear data, we need modern comparative data. Another matter that needs some consideration is whether all fossil teeth are useful for microwear analysis. Obviously, whenever well preserved enamel is not present, or when postmortem wear has altered the antemortem striation pattern, microwear interpretation is not possible. For the buccal surface of human teeth postmortem wear can be ruled out if isolated nonerupted teeth show no scratches or if a distinct nonrandom distribution of scratches is seen in any tooth. Also, no significant between-groups differences in the striation pattern should be expected if postmortem processes were responsible for the striations observed.

MATERIALS AND METHODS

Ten reference collections of modern hunting-gathering, pastoralist, and agriculturalist populations were studied in order to characterize a wide range of human populations, with distinct dietary habits, through the analysis of buccal tooth striation patterns. Also, a large sample of Middle and Upper Pleistocene human fossil remains was studied using the same methodology as for the modern samples.

The modern human sample

The modern human sample represents populations from different parts of the world, with different dietary habits, living under different ecological conditions. The samples studied consist of skull collections held at the British Museum (Natural History) of London, the Odontological Museum (Royal College of Surgeons) of London, and the Museo de la Plata (Argentina). Ten populations were included in the analysis and a total of 153 well preserved individuals were studied (Table 1). Most of the analyzed specimens were collected during the second half of the 19th century, mainly through private contributions. Specific information about each individual was available for many of the analyzed individuals (age, sex, origin, etc.), but for some of the skulls only an attribution to a particular human group was

TABLE 1. Original provenance and size of the modern humans sample and fossil remains studied[1]

Population	Provenance	Sample size
Agriculturalist Hindu	Farmers from Bihar and Orissa, Central India	20 inds.
Andamanese	Hunter-gatherers from the Andaman Islands, Gulf of Bengala	18 inds.
Fueguians	Hunter-gatherers from Tierra del Fuego, Argentina, and Chile	20 inds.
Bushmen	Hunter-gatherers from the Kalahari desert, mainly South Africa	15 inds.
Lapps	Nomadic pastoralists from Norway, Finland, and Russia	5 inds.
Inuit	Hunter-gatherers, mainly from Greenland	20 inds.
Veddahs	Hunter-gatherers from Sri Lanka	9 inds.
Tasmanians	Hunter-gatherers from Tasmania	11 inds.
Australian Aborigines	Hunter-gatherers from central, west, and north of Australia	18 inds.
Vancouver Islanders	Hunter-gatherers from the island of Vancouver, Canada	17 inds.
Archaic *H. sapiens*	Banyoles	(Banyoles, Spain)
	Montmaurin	(MH, Paris)
	Broken Hill	(BMNH, London)
	La Chaise Abrie Suard	(Bordeaux, France)
	La Chaise Burgeois et Delaunay	(Bordeaux, France)
Neanderthals	Malarnaud	(MH, Paris)
	St. Cesaire	(Bordeaux, France)
	Marillac	(MH, Paris)
	La Quina V	(MH, Paris)
	Amud 1	(RM, Israel)
	Tabun 1	(BMNH, London)
	Tabun 2	(Rm, Israel)
	Gibraltar 2	(BMNH, London)
Anatomically modern humans	Skhül 4	(RM, Israel)
	Qafzeh 9	(RM, Israel)
	Cromagnon 4	(MH, Paris)
	La Madelaine	(MH, Paris)
	Round-du-Barry	(MH, Paris)
	Veyrier-sous-Saleve	(MH, Paris)
	Abri-Pataud	(MH, Paris)

[1] Datings of fossil remains have not been included but they can be found in Stringer and Gamble (1993). MH stands for Musée de l'Homme; RM is the Rockfeller Museum; BMNH is the British Museum of Natural History.

present, with no further details. Whenever the skulls were not sexed we have attempted to sex them by using classical cranial traits, such as the supraorbital ridges, mastoid process, and nuchal crest (Ferembach et al., 1980; Brothwell, 1981; Bass, 1986). Except for three juvenile Bushmen skulls, only adult individuals were studied, in order to control for age variability of the striation pattern (Pérez-Pérez et al., 1994). Adult ages were estimated using cranial sutures, overall dental wear, and alveolar condition (Brothwell, 1981). Historical and museum records were also used whenever possible. Unfortunately, circumstances of death were rarely available. This type of data may provide important information to assess whether the individual might have changed his or her traditional dietary habits before death. In addition, successive removals from one museum to another might have led to classification errors in the museum records. However, most of the specimens show identification numbers painted on the skull during the 19th century, and it is unlikely that such errors are critical for the analysis done here.

Museum collections usually lack valuable information that may be essential for interpreting tooth microwear, as Teaford and Runestad (1992) have pointed out. However, although museum samples have important biases, they are of great importance if no other research materials are available, especially for studies concerning the variability of human diet. We must be aware that, at present, almost all hunter-gatherer groups have dramatically changed or abandoned their traditional way of subsistence. Moreover, some aboriginal groups, such as the Fueguians or the Tasmanians, have already disappeared and the archaeological record of most of these groups is scarce and fragmentary.

Human groups with a characteristic biological and ethnological identity were selected, although some of them were highly heterogeneous. The so-called Fueguians, for instance, included three hunter-gather

groups (Selknam, Kawesker, and Yamana), and the Indians from Vancouver Island include individuals from different Indian tribes and probably from adjacent areas. However, groups so closely related are likely to have similar diets, and are probably homogeneous from an ecological and dietary perspective. Two groups without a hunter-gatherer strategy, the Lapps and the Hindus, have been included in the sample. Lapps are nomadic pastoralists, whose diet was mainly based on reindeer herding (Reader, 1988). They lived in the northern latitudes in Europe, where plant food materials are only seasonally available. The Hindu sample consists of individuals from the regions of Bihar and Orissa, with an exclusively vegetarian diet (based on rice) due to religious reasons. The Inuit have been traditionally considered an exclusively hunting group, with almost no vegetable intake (De Poncins, 1941; Vanstone, 1962; Draper, 1978). The Fueguians were primarily dependent on hunting and fishing (Gusinde, 1937; Orquera et al., 1977; Chapman, 1986), as were the Indians from Vancouver, for whom fish (especially salmon) and sea mammals were the most important food resources (Suttles, 1968; Lazenby and McCormack, 1985). The Andaman Islanders, Australian Aborigines, Veddhas, Bushmen, and Tasmanians were hunter-gatherer populations, from both tropical forest and arid environments (Table 1). Despite the classical carnivorous image of hunter-gatherer populations, extensive research among hunter-gatherer groups from tropical climates has shown that these people are more inclined to gather than to hunt, since hunting is not always available or certain (Lee and DeVore, 1968). Studies of Bushmen (Lee, 1973; Lee and DeVore, 1976) conclude that vegetable matter is generally about 60–80% of the total diet by weight, and that about 67% of the calories and proteins have a vegetable origin. In Pygmies, a hunter-gatherer group from the tropical forest, the proportion is even higher, about 70% (Hart, 1978). However, the lack of ecological and ethnographical information for some of these groups allows us to classify them only into hunter-gatherers from forested or arid environments.

For methodological reasons we have established four broad dietary categories that can be justified from ecological and environmental points of view. Although this classification can be seen as an oversimplification, dietary differences between groups may be expected. Therefore, this procedure may help in the characterization of the populations studied and in the interpretation of the microwear data. The four groups considered were: (1) agriculturalist, Hindu sample (20 individuals); (2) hunter-gatherer, populations form a tropical forest environment, and including the Andamanese and Veddahs (44 individuals); (3) carnivorous hunter-gatherer and pastoralist populations, including Fueguans, Inuit, Vancouver Islanders, and Lapps (62 individuals); and (4) hunter-gatherer populations from arid and mesothermal environments, including Bushmen, Austrialian Aborigines, and Tasmanians (27 individuals).

This broad classification of the hunter-gatherer populations tends to correspond with the geographic latitude where they lived. The tropical forest populations (group 2) lived around 10° latitude, the arid and mesothermal environment populations (group 4) lived between 25° and 42° latitude, and the carnivorous ones (group 3) lived between 50° and 70° latitude, approximately. A linear correlation between distance from the equator and subsistence strategy has been described by Lee and DeVore (1968).

Fossil remains

Several human fossil remains have also been studied (Table 1) using the same methodology as for the reference collections. All fossil materials represent adult individuals, with the exception of the Gibraltar child (Devil's Tower), for which the first deciduous molar was analyzed. The reasons for including this subadult individual in our sample have already been discussed in Lalueza and Pérez-Pérez (1993). The fossil sample is highly heterogeneous in terms of its geographical origin and dating, and different dietary specializations are expected to be present.

Regarding the samples from the Near East, there is a general consensus that the hominids at Tanbun-Amud (Tabun 1, Tabun 2, Amud 1) might best be classified as Neanderthals, while the Qafzeh-Skhül hominids (Qafzeh 9, Skhül 4) are probably modern hu-

mans (Stringer, 1978; Stringer et al., 1984; Suzuki and Takai, 1970; Vandermeersch, 1981). The fossil remains from Gibraltar (Devil's Tower), Marillac, Malarnaud, La Quina V, and St. Cesaire are usually described as belonging to the European Neanderthal group (Stringer et al., 1984). Nevertheless, Malarnaud might date to the Riss-Würm interglacial period (Amadei and Navari, 1986), and its attribution to the Neanderthals may be debatable. St. Cesaire is a special case because of the late dating of this specimen, which has the morphology of the *classic* Neanderthals and yet is associated with Upper Paleolithic tools (Vandermeersch, 1984). The Middle Pleistocene fossils of La Chaise Suard show clear Neanderthal affinities, and the specimens from La Chaise Bougeois et Delaunay, from the last interglacial Riss-Würm time period (Amadei and Navari, 1986), although clearly Neanderthal related, lack the full *classic* morphological configuration (Trinkaus, 1988). Banyoles has been usually attributed to the ante-Neanderthal group, lacking Neanderthal apomorphies (Lumley, 1973). However, its current minimum dating (45,000 B.P.) is fairly late (Julià and Bischoff, 1991). Montmaurin has been considered an ante-Neanderthal specimen (Lumley, 1973), but might date to the Würm I glacial period (Amadei and Navari, 1986). Broken Hill is in the center of a debate and alternatively has been considered as either a late *H. erectus* or an early *H. sapiens* (Day, 1986). Finally, the Cro-Magnon 4 (Day, 1986), Abri-Pataud (Stringer et al., 1984), Veyrier (Ferembach et al., 1986), La Madelaine (Bouvier, 1972), and Rond-du-Barry (Bayle des Hermens and Heim, 1989) specimens, all of them *H. sapiens sapiens,* belong to the Upper Paleolithic. Broad taxonomic grouping of the fossil remains into archiaci *H. sapiens,* Neanderthals, and anatomically modern humans (Table 1) has been undertaken.

Data collection

One tooth per individual (Pérez-Pérez et al., 1994) was analyzed by scanning electron microscopy (SEM). Only individuals not affected by gross oral pathologies were considered in order to exclude abnormal striation patterns due to pathological conditions (Lalueza and Berkovitz, 1992). Either mandibular or maxillary teeth (M1, M2, and Pm4) were considered for the analysis. The modern sample consists of 153 teeth: 133 (86.9%) M1, 15 (9.8%) M2, and 5 (3.3%) Pm4; 78 were mandibular teeth and 75 were maxillary teeth; 70 belong to males, 59 to females, and 24 to individuals for which sex classification was not available; 59 were right-side teeth and 94 were left-side teeth. The fossil sample includes 20 teeth: one deciduous m1, three Pm4, 13 M1, two M2, and one M3; 14 were left-side teeth and six were right-side teeth; 16 were mandibular teeth and four were maxillary teeth. The sample of fossils is obviously somewhat more heterogeneous, due to differences in the preservation of the specimens.

Molds of the buccal surfaces of teeth were obtained using Triafol plastic (Balzers Union BU 008 002 T) dissolved in chloroform at 50 g/l concentration. The mold covered the intermediate third of the tooth (avoiding the occlusal and cervical thirds), in the mesial half of the buccal surface, approximately 3–6 mm occlusal to the cementoenamel junction. With this procedure we tried to avoid the problems of intradental variability described by Fine and Craig (1981). The molds were sputter coated with a 400 Å gold layer and observed with a Hitachi S-2300 scanning electron microscope. Each mold was photographed at 100× magnification, 20 KV accelerating voltage, and 0° of tilt angle, covering an area of approximately 1 mm^2. The methodology used was the same as in our previous studies (see Lalueza and Pérez-Pérez, 1993, and Pérez-Pérez et al., 1994, for a detailed description). The length (in micrometers) and orientation (from 0° to 180° with reference to the occlusal plane) of each striation on the buccal surface were recorded using an IBAS 2 Image Analyzer System. For methodological standardization the length of the striations was recorded within the surveyed area, although some of them surpassed the limits of the SEM photograph. Four categories of orientation were considered: vertical (67.5°–112.5°), mesio-occlusal to distocervical (112.5°–157.5° for the lower left and upper right teeth; 22.5°–67.5° for the lower right and upper left teeth), disto-occlusal to mesiocervical (22.5°–67.5° for the

TABLE 2. Kolmogorov–Smirnov two-tail normality tests for the 15 variables studied[1]

		Agriculturalist Hindus			Hunter-gatherers Tropical forest			Hunter-gatherers Carnivorous			Hunter-gatherers Arid environment			All groups		
		Z	*P*	n	Z	*P*	n	Z	*P*	n	Z	*P*	n	Z	*P*	n
	Disto-occlusal to mesiocervical striations															
1	Number	0.601	0.863	20	0.934	0.348	44	1.304	0.067	62	0.678	0.748	27	1.531	0.018[2]	153
2	Length	0.446	0.989	20	0.385	0.998	44	0.926	0.357	62	0.772	0.590	27	1.055	0.216	153
3	SD	0.436	0.991	19	0.627	0.826	44	0.743	0.639	59	0.579	0.890	27	0.974	0.299	149
	Horizontal striations															
4	Number	0.478	0.977	20	1.033	0.236	44	1.591	0.013[2]	62	0.648	0.795	27	1.473	0.026[2]	153
5	Length	1.051	0.219	20	1.247	0.089	44	0.951	0.327	60	0.880	0.420	27	1.527	0.019[2]	151
6	SD	0.564	0.908	20	0.569	0.903	44	0.798	0.548	54	0.710	0.695	27	1.030	0.239	153
	Mesio-occlusal to distocervical striations															
7	Number	0.820	0.512	20	0.993	0.277	44	1.484	0.024[2]	62	0.787	0.566	27	1.570	0.014[2]	153
8	Length	0.496	0.966	20	0.695	0.720	44	0.730	0.660	62	0.882	0.418	27	1.390	0.042[2]	153
9	SD	0.761	0.609	19	1.079	0.194	44	0.742	0.641	60	0.816	0.518	27	1.342	0.054	150
	Vertical striations															
10	Number	0.692	0.725	20	0.573	0.898	44	0.676	0.750	62	0.675	0.753	27	1.044	0.226	153
11	Length	0.529	0.943	20	0.710	0.694	44	0.651	0.790	62	0.690	0.727	27	1.374	0.046[2]	153
12	SD	0.696	0.719	20	0.489	0.971	44	0.726	0.667	61	0.853	0.460	27	0.886	0.412	152
	All striations															
13	Number	0.943	0.336	20	1.001	0.269	44	1.222	0.101	62	0.865	0.443	27	0.729	0.662	153
14	Length	0.935	0.347	20	0.674	0.753	44	0.843	0.477	62	1.100	0.177	27	1.368	0.047[2]	153
15	SD	0.583	0.886	20	0.436	0.991	44	1.373	0.046[2]	62	1.164	0.133	27	0.803	0.540	153

[1] SD, standard deviation of the length of the striations. Sample sizes vary because a 0 value is considered a missing value for the average length and standard deviation of the length of the striations. Z represents the normality test score; *P* is the probability of the test; n is the sample size.
[2] Indicates significance at 5% confidence level.

lower left and upper right teeth; 112.5°–157.5° for the lower right and upper left teeth), and horizontal (0°–22.5° and 157.5°–180°) (Pérez-Pérez et al., 1994). Fifteen summary variables (Table 2), measuring the number of striations, length of striations, and variability (standard deviation) of the length, by orientation groups, were derived for each individual (Pérez-Pérez et al., 1994). All the analysis and numerical calculations were made without knowing which specimen was being analyzed, in order to avoid any possible observer bias.

Data analysis

Summary variables for each orientation were obtined and summary statistics of these variables were calculated for each population considered. Thus, the microwear pattern of each analyzed individual was characterized by 15 summary variables for the number, average length, and standard deviation of the length of the observed striations by groups of orientation: (1) NV, number of vertical striations; (2) NH, number of horizontal striations; (3) NMD, number of mesio-occlusal to distocervical striations; (4) NDM, number of disto-occlusal to mesiocervical striations; (5) NT, total number of striations; (6) XV, average length of the vertical striations; (7) XH, average length of the horizontal striations; (8) XMD, average length of the mesio-occlusal to distocervical striations; (9) XDM, average length of the disto-occlusal to mesiocervical striations; (10) XT, average length of all striations; (11) STDV, standard deviation of the length of the vertical striations; (12) STDH, standard deviation of the length of the horizontal striations; (13) STDMD, standard deviation of length of the mesio-occlusal to distocervical striations; (14) STDDM, standard deviation of length of the disto-occlusal to mesiocervical striations; and (15) STDT, standard deviation of the length of all the striations.

Indexes of relative frequently of striations by orientation were calculated for the fossil specimens and the modern samples by dividing the number of horizontal and vertical striations by the total number of observed striations (NH/NT, NV/NT). An index of the number of horizontal to vertical striations (NH/NV) was also calculated.

The normality of the frequency distributions for the variables considered was tested with the Kolmogorov–Smirnov test for goodness of fit (Sokal and Rohlf, 1981, pp. 716–

721). The interpopulation comparisons of the microwear measurements were done with factorial analysis of variance (factoral ANOVA) both for a single factor and higher-order interactions (Norusis, 1988, pp. 127–136). All tests were performed with the SPSS-PC + v. 3.1 statistical package. The factorial ANOVAs were used to test for interpopulation differences in the average number, length, and length variability of the observed striations. The factors used were population, sex, tooth side, and jaw. The expectation was that populations with distinct dietary habits, living under different ecological conditions, would show a characteristic microwear pattern, and that the intrapopulation variability would be significantly smaller than the interpopulation variability. A similar and consistent pattern should be obtained for those populations having similar diets. Sexual differences in the striation pattern may also be present if a significantly different pattern of access to food resources exists within one population.

If the factorial analysis of variance shows significant differences among the samples considered, discriminant functions could be derived with a multivariate discriminant analysis. These functions might, then, be applied to fossil remains in order to infer their dietary habits.

RESULTS

Only the carnivorous hunter-gatherer group shows deviations from normality (at a 5% confidence level) for some of the variables analyzed: number of horizontal and mesio-occlusal to distocervical striations, and length variability of all striations (Table 2). None of the 15 summary variables studied differs significantly from normality for the other dietary groups (agriculturalists, hunter-gatherers from arid and mesothermal environment, hunter-gatherers from tropical forest) considered, though many deviations are obtained if all groups are considered together (Table 2). Although the length of the striations has been previously found to follow a log-normal distribution (Pérez-Pérez et al., 1994), none of the calculated summary variables for the length of the striations analyzed here differ from normality.

The average density of striations varies approximately from 30 to 75 per analyzed tooth, with an overall average of 55.4 (Table 3). By orientations, the average number of striations also varies considerably among the 10 populations considered. The average length of all the observed striations is high (190.1 μm) and the vertical striations are in general longer than the other striations (Table 3). If the samples are grouped by dietary habits (Table 4), high variability among groups can still be seen. A factorial analysis of variance for the main effects of group (carnivorous hunter-gatherer, hunter-gatherer from tropical forest, hunter-gatherer from arid-mesothermal environment, agriculturalists), sex (female, male), side (left and right teeth), jaw (mandibular and maxillary teeth), and tooth (Pm4, M1, M2) differences were also tested (Table 5) with factorial ANOVAs for the effect of sex, and some significant tests for the length of the striations were found out of the 60 comparisons made by group and striation orientation. No significant sex-related differences were found for the number of striations (Table 5).

If the 10 samples considered are compared using a single-factor one-way analysis of variance (ONEWAY) for the 15 variables considered, the frequency of significant tests obtained in a two-by-two comparison can be used as a dissimilarity index between the samples compared. The significance between pairs of groups was calculated using the LSD (Least Square Distance) distance for the ONEWAY ANOVA instead of the MODLSD (Modified LSD) because the MODLSD, although suitable for multiple comparisons within the ANOVA analysis, is more conservative when finding significant differences between pairs of groups (Norusis, 1988). If two groups do not significantly differ, at a 5% confidence level, for any of the 15 variables considered, the dissimilarity index for that comparison would be 0, but if the two groups compared significantly differ for all of the analyzed variables, the index would be 1. Although this can be considered only a rough indicator of dissimilarity between groups, it can be used to compute a similarity tree for the 10 samples considered using a cluster analysis (Fig. 1B). The dendrogram obtained may vary depending

TABLE 3. Summary statistics of number, length, and length variability for the studied samples[1]

Analyzed samples	Disto-occlusal to mesiocervical			Horizontal			Mesio-occlusal to distocervical			Vertical			All		
	Number of striations														
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n
Fueguians	6.6	3.1	20	4.0	2.3	20	6.2	4.5	20	16.4	9.3	20	32.0	67.9	20
Inuit	9.7	8.6	20	4.3	2.8	20	7.5	5.3	20	17.0	7.8	20	38.7	18.5	20
Vancouver	10.9	6.1	17	3.4	2.4	17	7.2	6.1	17	20.2	8.5	17	41.7	16.0	17
Lapps	7.0	7.3	5	5.2	3.6	5	7.2	2.8	5	16.0	9.0	5	35.4	14.9	5
Andamanese	19.0	10.7	18	22.1	8.4	18	9.1	4.4	18	24.7	11.5	18	74.8	20.5	18
Veddahs	18.3	8.3	9	22.7	9.4	9	9.2	3.2	9	24.0	15.3	9	74.2	28.0	9
Bushmen	15.1	7.6	15	20.5	9.6	15	12.4	6.0	15	19.7	7.7	15	67.9	16.7	15
Tasmanians	18.3	12.0	11	15.5	6.9	11	11.6	4.9	11	28.0	10.6	11	73.4	29.0	11
Australians	16.9	6.8	18	13.1	5.0	18	12.5	5.6	18	23.6	7.9	18	66.2	11.0	18
Hindus	8.3	4.4	20	29.4	12.4	20	6.4	3.6	20	13.4	8.1	20	57.4	17.8	20
All	12.8	8.7	153	14.1	11.7	153	8.8	5.3	153	19.9	10.1	153	55.4	24.1	153
	Length of striations														
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n
Fueguians	224.5	84.6	20	166.1	60.2	20	176.9	58.7	20	248.0	60.9	20	223.1	51.4	20
Inuit	143.6	69.5	20	130.4	61.1	18	138.8	46.0	20	214.8	44.0	20	193.3	37.5	20
Vancouver	209.7	60.7	17	181.0	91.8	17	225.3	70.1	17	264.4	59.7	17	235.2	48.8	17
Lapps	235.9	23.7	5	136.2	43.3	5	176.1	74.9	5	211.5	82.7	5	228.1	50.2	5
Andamanese	144.7	37.1	18	139.4	41.9	18	127.6	32.4	18	169.2	34.8	18	156.2	26.5	18
Veddahs	158.3	32.8	9	202.1	79.8	9	148.5	44.2	9	211.0	52.5	9	193.7	57.2	9
Bushmen	179.4	47.6	15	150.5	19.9	15	161.3	41.7	15	204.5	49.4	15	176.4	26.6	15
Tasmanians	146.7	34.9	11	157.0	87.2	11	134.5	33.4	11	191.8	41.5	11	169.1	40.0	11
Australians	148.5	35.3	18	128.7	36.6	18	126.9	36.2	18	174.7	38.2	18	152.0	28.1	18
Hindus	140.5	40.3	20	219.6	78.2	20	150.3	46.3	20	157.6	42.9	20	191.1	49.6	20
All	169.4	62.0	153	161.9	69.1	151	155.8	55.8	153	204.1	59.1	153	190.1	49.2	153
	Standard deviation of the length														
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n
Fueguians	121.4	72.3	20	81.5	39.2	19	85.4	60.9	19	129.1	46.5	20	130.0	39.8	20
Inuit	81.3	51.3	19	67.6	44.2	18	75.0	61.7	20	117.4	59.2	20	116.5	52.8	20
Vancouver	108.3	52.3	16	64.0	60.4	13	100.3	48.1	16	143.5	41.4	17	139.8	32.3	17
Lapps	145.8	29.4	4	44.2	36.9	4	93.8	51.6	5	119.8	43.2	4	142.3	31.0	5
Andamanese	66.6	37.3	18	71.7	27.6	18	65.9	31.8	18	104.3	35.7	18	94.4	23.4	18
Veddahs	99.3	44.1	9	133.8	52.2	9	88.5	42.8	9	136.4	57.0	9	130.3	48.6	9
Bushmen	106.8	53.1	15	100.4	34.2	15	91.4	53.8	15	119.8	43.2	15	118.1	23.1	15
Tasmanians	87.1	36.9	11	103.6	59.8	11	69.3	34.2	11	123.7	47.1	11	119.1	39.8	11
Australians	105.1	40.9	18	65.2	33.7	18	80.3	48.3	18	113.9	36.9	18	107.8	27.1	18
Hindus	74.8	36.4	19	133.0	49.1	20	67.7	53.7	19	90.3	39.2	20	130.5	38.9	20
All	95.7	51.5	149	87.9	50.2	145	80.3	50.4	150	118.7	46.6	152	121.0	38.5	153

[1] Sample size (n) indicates number of analyzed individuals. The raw (non-log-transformed) data has been used since most normality tests are not significant (Table 2). If no striations were present, the value of 0 was not considered a missing value since the absence of striations for any specific orientation may be informative of interpopulational differences.

on the type of grouping criteria used. To counter this effect, seven grouping criteria were used (Norusis, 1988): average linkage (both between groups and within groups), single linkage, complete linkage, centroid method, median method, and Ward method. All the methods grouped the four carnivorous populations (Fueguains, Inuit, Lapps, and Vancouver Islanders) separately from the other hunter-gatherer groups (Bushmen, Tasmanians, Australian aborigines, Andaman Islanders, and Veddahs). Four of the analyses classified the Hindu group as independent from the other two groups. The average linkage within groups method classified the Hindu sample within the noncarnivorous hunter-gatherers, and the complete linkage and Ward methods classified the Hindu sample close to the Inuit, within the carnivore group. Figure 1A shows the expected ecological and dietary grouping of the samples, which closely resembles the obtained clusters, using the average linkage between groups method (Fig. 1B). Figure 1C,D shows cluster analysis classifications (for the Ward and complete grouping criteria, respectively) of the 10 samples considered, entering the mean values of the 15 variables into the analysis for computing Euclidean distances between populations. The results obtained are very similar to those obtained with the dissimilarity index (Fig. 1B).

Interpopulation variability

Since the striation pattern seems to parallel the dietary and ecological grouping of the

TABLE 4. Summary statistics of number, length, and length variability by group and sex[1]

Analyzed groups	Disto-occlusal to mesiocervical			Horizontal			Mesio-occlusal to distocervical			Vertical			All		
	Number of striations														
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n
Hindu	8.3	4.4	20	29.4	12.4	20	6.4	3.6	20	13.4	8.1	20	57.4	17.8	20
Female	5.6	4.0	7	24.7	9.6	7	7.6	3.6	20	9.3	4.4	7	47.1	14.2	7
Male	9.8	4.1	13	31.8	13.3	13	5.8	3.5	13	15.5	8.9	13	62.9	17.5	13
Arid HG	16.6	8.4	44	16.2	7.9	44	12.3	5.4	44	23.4	8.9	44	68.5	18.5	44
Female	20.1	8.1	14	18.1	11.2	14	12.2	4.7	14	24.6	8.6	14	75.1	19.5	14
Male	16.3	9.6	18	15.9	3.8	18	12.3	5.9	18	22.0	10.1	18	66.7	20.3	18
?	13.0	5.6	12	14.5	7.9	12	12.3	6.0	12	23.9	7.7	12	63.8	12.9	12
Carnivor HG	8.8	6.6	62	4.0	2.6	62	6.9	5.1	62	17.6	8.5	62	37.1	16.2	62
Female	8.7	6.1	24	3.8	3.1	24	6.3	3.7	24	15.1	8.3	24	33.8	15.2	24
Male	9.0	7.1	30	4.1	2.1	30	7.7	6.3	30	18.9	8.4	30	39.2	16.9	30
?	8.4	6.8	8	4.6	2.8	8	6.0	3.0	8	20.1	8.8	8	39.1	16.6	8
Tropical HG	18.8	9.8	27	22.3	8.5	27	9.1	3.9	27	24.4	12.6	27	74.6	22.7	27
Female	19.7	9.3	14	20.7	7.1	14	9.5	4.6	14	27.3	11.5	14	77.2	19.4	14
Male	18.0	11.3	9	20.6	9.0	9	8.3	3.2	9	19.4	11.1	9	66.3	23.9	9
?	17.3	10.0	4	31.8	7.5	4	9.5	3.7	4	25.8	18.9	4	84.3	31.0	4
All	12.8	8.7	153	14.1	11.7	153	8.8	5.3	153	19.9	10.1	153	55.4	24.1	153
Female	13.6	9.4	59	13.7	11.2	59	8.6	4.7	59	19.6	10.8	59	55.5	26.3	59
Male	12.2	9.7	70	14.4	12.4	70	8.6	5.8	70	19.1	9.4	70	54.2	22.6	70
?	12.2	7.2	24	14.1	11.2	24	9.7	5.5	24	23.0	10.2	24	59.0	23.5	24
	Length of striations														
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n
Hindu	140.5	40.3	20	219.6	78.2	20	150.3	46.3	20	157.6	42.9	20	191.1	49.6	20
Female	134.1	49.4	7	272.1	103.6	7	143.5	43.2	7	177.0	56.3	7	222.2	66.6	7
Male	144.0	36.2	13	191.3	42.9	13	153.9	49.2	13	147.1	31.5	13	174.4	28.3	13
Arid HG	158.6	41.8	44	143.2	50.8	44	140.5	39.8	44	189.2	44.1	44	164.6	32.2	44
Female	153.9	32.0	14	149.0	80.1	14	133.7	37.8	14	180.3	27.5	14	163.1	34.3	14
Male	151.8	37.0	18	142.0	28.8	18	142.4	33.4	18	184.2	51.1	18	160.0	34.1	18
?	174.1	56.0	12	138.3	34.2	12	145.6	51.7	12	206.9	46.8	24	173.4	27.2	24
Carnivor HG	195.3	78.0	62	157.1	71.4	60	177.8	67.2	62	238.8	60.0	62	217.2	48.5	62
Female	164.7	55.3	24	157.5	86.2	22	146.7	43.4	24	205.8	49.3	24	191.3	41.4	24
Male	205.2	86.6	30	148.4	61.3	30	191.8	73.6	30	253.1	56.3	30	228.1	46.3	30
?	249.7	69.9	8	188.9	60.3	8	218.6	68.5	8	284.3	57.3	8	254.0	40.3	8
Tropical HG	149.2	35.7	27	160.3	63.4	27	134.5	37.3	27	183.1	45.2	27	168.7	42.3	27
Female	153.2	36.8	14	142.5	45.4	14	129.3	30.8	14	182.4	34.2	14	161.8	30.6	14
Male	138.6	32.4	9	164.3	75.2	9	139.3	53.3	9	171.0	49.6	9	165.3	53.0	9
?	159.4	42.6	4	213.9	73.7	4	142.3	7.9	4	212.9	66.2	4	200.8	47.8	4
All	169.4	62.0	153	159.8	71.1	153	155.8	55.8	153	204.1	59.1	153	190.1	49.2	153
Female	155.8	45.7	59	160.2	90.6	59	139.1	39.1	59	190.8	43.4	59	181.2	45.0	59
Male	171.5	68.7	70	156.8	55.5	70	165.3	62.1	70	205.2	65.8	70	192.5	51.4	70
?	196.8	68.6	24	167.8	57.9	24	169.4	63.1	24	233.7	62.9	24	204.8	50.0	24
	Standard deviation of the length														
	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n	x̄	SD	n
Hindu	74.8	36.4	19	133.0	49.1	20	67.7	53.7	19	90.3	39.2	20	130.5	38.9	20
Female	63.6	34.1	6	156.6	50.0	7	83.1	44.2	6	83.9	34.9	7	146.6	52.1	7
Male	80.0	37.6	13	120.2	45.5	13	60.6	57.8	13	93.8	42.2	13	121.8	28.4	13
Arid HG	101.2	44.3	44	86.8	44.7	44	81.3	47.0	44	118.4	41.0	44	114.1	29.4	44
Female	108.8	34.4	14	94.1	56.8	14	93.5	53.0	14	111.5	30.4	14	117.9	27.8	14
Male	95.2	45.3	18	79.8	32.2	18	75.3	38.8	18	117.6	42.2	18	106.8	30.7	18
?	101.5	54.5	12	88.7	46.6	12	76.0	52.1	12	127.5	50.6	12	120.7	29.0	12
Carnivor HG	106.6	60.6	59	69.9	46.5	54	86.6	56.8	60	130.0	49.7	61	129.3	42.4	62
Female	80.2	46.3	23	66.9	49.2	18	70.4	51.6	24	110.1	54.2	23	113.2	42.3	24
Male	122.9	69.0	28	60.7	38.6	29	91.3	51.7	28	139.7	45.4	30	137.5	42.9	30
?	125.3	40.0	8	115.5	49.1	7	118.5	77.4	8	150.4	34.2	8	147.0	24.8	8
Tropical HG	77.5	41.9	27	92.4	47.2	27	73.4	36.6	27	115.0	45.5	27	106.4	37.1	27
Female	77.9	41.2	14	76.4	39.1	14	67.6	33.1	14	115.7	32.4	14	100.6	26.6	14
Male	65.3	30.3	9	90.9	26.2	9	77.8	49.2	9	106.1	51,6	9	98.7	31.7	9
?	103.3	63.9	4	155.6	64.4	4	83.9	7.9	4	132.5	75.0	4	143.9	63.1	4
All	93.2	53.1	153	83.3	52.6	153	78.7	51.2	153	117.9	47.4	153	121.0	38.5	153
Female	82.0	44.8	59	79.2	59.2	59	75.3	48.0	59	106.8	44.4	59	115.3	38.7	59
Male	96.9	58.7	70	79.7	43.3	70	77.1	50.8	70	121.2	47.4	70	121.7	38.7	70
?	109.7	50.7	24	104.0	57.5	24	91.6	59.3	24	135.9	49.2	24	133.3	35.7	24

[1] Sample size varies depending on missing values and indicates number of individuals considered. Group classification was based on ecological and dietary information from ethnographic records.

TABLE 5. Factorial analyses of variance for the main effects of group, sex, side, jaw, and tooth[1]

		Vertical		Total		Horizontal		Mesio-occlusal to distocervical		Disto-occlusal to mesiocervical	
Variable	Effect of	F	P	F	P	F	P	F	P	F	P
Number	Main effects	6.382	0.000*	13.394	0.000*	26.056	0.000*	4.016	0.000*	6.279	0.000*
"	Group	10.246	0.000*	34.153	0.000*	68.491	0.000*	10.445	0.000*	15.354	0.000*
"	Sex	0.000	0.993	0.020	0.887	0.010	0.921	0.424	0.516	0.165	0.685
"	Side	6.141	0.015*	1.526	0.219	0.008	0.927	0.568	0.453	0.828	0.365
"	Jaw	5.716	0.018*	0.326	0.569	0.868	0.353	0.018	0.894	0.807	0.371
"	Tooth	3.412	0.036	2.286	0.106	0.647	0.526	1.234	0.295	0.023	0.977
Length	Main effects	6.255	0.000*	4.677	0.000*	3.151	0.003*	2.549	0.014*	2.423	0.018*
"	Group	15.122	0.000*	11.594	0.000*	6.128	0.001*	3.275	0.024*	4.728	0.004*
"	Sex	2.720	0.102	1.562	0.214	0.769	0.382	7.309	0.008*	2.049	0.155
"	Side	0.965	0.328	0.342	0.560	0.168	0.683	0.153	0.697	0.406	0.525
"	Jaw	0.000	0.989	0.050	0.823	0.496	0.483	0.374	0.542	4.287	0.041*
"	Tooth	0.062	0.940	0.425	0.655	2.258	0.109	0.732	0.483	0.134	0.875
SD	Main effects	1.960	0.057	2.066	0.044*	5.616	0.000*	0.720	0.673	2.555	0.013*
"	Group	3.658	0.014*	3.000	0.033*	11.821	0.000*	0.976	0.407	3.569	0.016*
"	Sex	2.658	0.106	0.664	0.417	1.150	0.286	0.043	0.837	3.077	0.082
"	Side	0.004	0.948	0.013	0.910	0.309	0.579	0.556	0.457	0.069	0.793
"	Jaw	1.838	0.178	1.610	0.207	1.005	0.318	0.289	0.592	7.105	0.009*
"	Tooth	0.241	0.786	1.494	0.229	2.443	0.091	1.603	0.206	0.190	0.827

Effect of sex

		Vertical		Total		Horizontal		Mesio-occlusal to distocervical		Disto-occlusal to mesiocervical	
Variable	Group	F	P	F	P	F	P	F	P	F	P
Number	Hindus	3.008	0.100	4.157	0.056	1.558	0.228	3.298	0.087	3.078	0.097
"	Tropical H-G	2.605	0.121	1.441	0.243	0.002	0.963	0.443	0.513	0.157	0.696
"	Arid H-G	0.609	0.441	1.400	0.246	0.596	0.446	0.001	0.974	1.430	0.241
"	Carnivorous	1.997	0.164	1.537	0.221	0.608	0.440	1.816	0.184	0.109	0.743
Length	Hindus	2.371	0.141	5.159	0.036*	6.187	0.023*	0.002	0.963	0.000	0.983
"	Tropical H-G	0.427	0.520	0.041	0.841	0.762	0.393	0.330	0.572	0.946	0.342
"	Arid H-G	0.066	0.799	0.065	0.800	0.117	0.734	0.480	0.494	0.028	0.869
"	Carnivorous	8.873	0.004*	9.271	0.004*	0.157	0.694	7.900	0.007*	6.559	0.014*
SD	Hindus	0.281	0.603	1.942	0.180	2.734	0.116	0.706	0.413	0.819	0.378
"	Tropical H-G	0.300	0.590	0.023	0.881	1.092	0.308	0.354	0.558	0.624	0.438
"	Arid H-G	0.206	0.653	1.105	0.301	0.800	0.378	1.260	0.271	0.877	0.356
"	Carnivorous	4.659	0.036*	4.321	0.043*	0.226	0.637	2.110	0.153	6.447	0.014*

[1]The top table consists of a factorial analysis of variance for a five-factors model. The group factor includes the four groups considered: agriculturalist, carnivorous hunter-gatherer, hunter-gatherer from tropical forest, and from arid environment. The other factors are: sex (female, male), side (left, right), jaw (mandible, maxilla), and tooth (Pm4, M1, M2). The bottom table consists of factorial analyses of variance, for a single-factor model of sex, separately for each group considered. An asterisk (*) stands for significance at a 5% confidence level.

studied samples, a stepwise discriminant analysis for the four diet groups was undertaken (Table 6). A total of 138 individuals were included in the analysis; 15 individuals were exluded due to missing values, The absence of striations was not considered a missing value for the number of striations because this was a typical trait of some individuals, especially in the carnivorous group. An average length of 0 was considered a missing value, and a 0 value for the average standard deviation (caused by either the absence of striations or the presence of only one striation) was also considered a missing value. A stepwise variable selection method was used to determine the most relevant variables for the characterization of the striation pattern.

The first variable to enter the analysis was the number of horizontal striations. The variable number of disto-occlusal to mesiocervical striations was removed from the analysis at step 10. Seven varibles did not meet the selection criteria (tolerance of 0.001) and thus were excluded from the analysis. After 10 steps only eight variables out of the 15 analyzed were included in the analysis (Table 6). The selection rule was to maximize the minimum Mahalanobis distance (D^2) between groups. The first two factors obtained account for 93.54% of the total variance. Factor 1 has a canonical correlation of

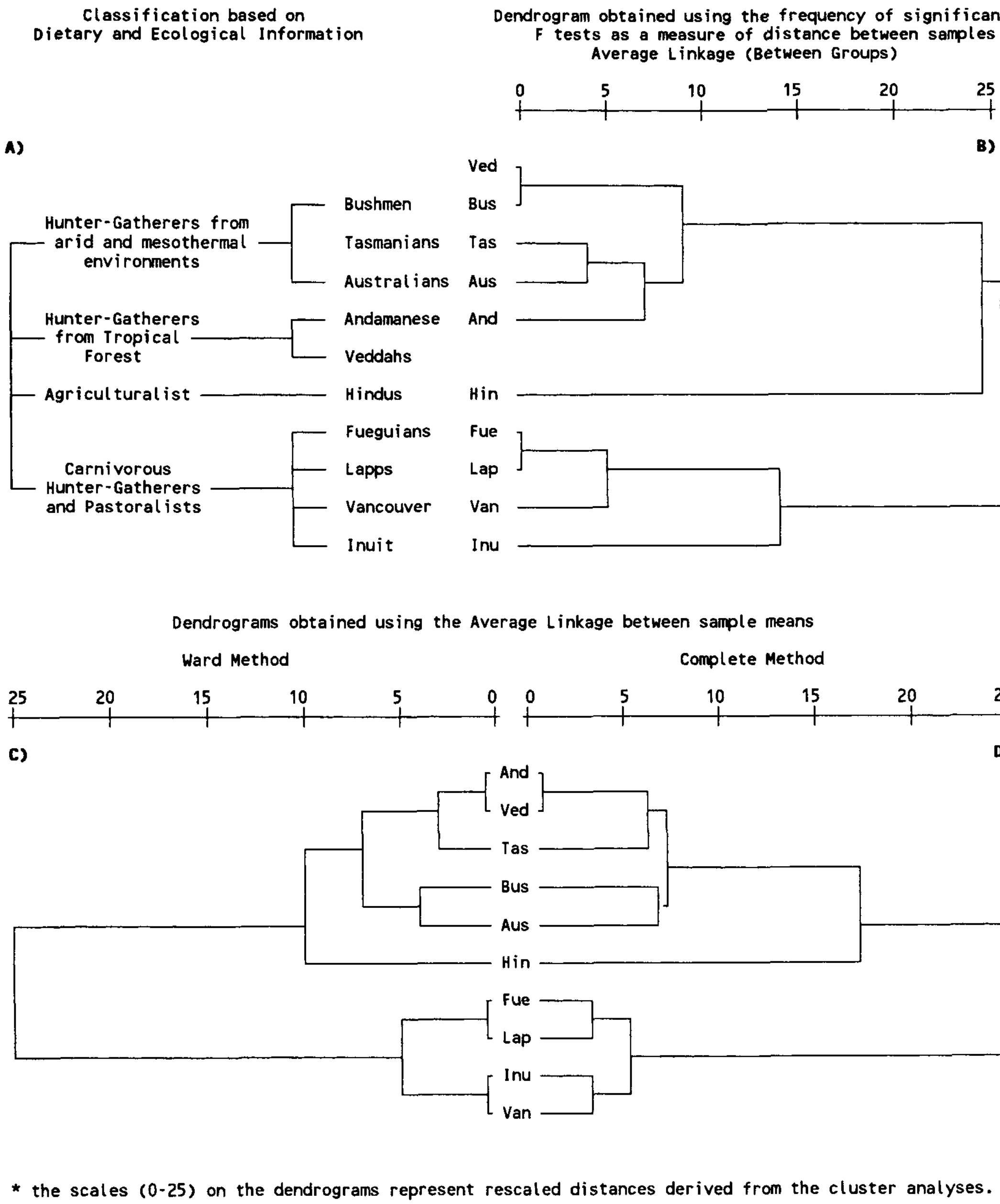

Fig. 1. **A:** Expected classification of the samples studied based on echological and ethnographical information. **B:** Cluster classification using one-way analyses of variance as disimilarity coefficients; the dendrogram was derived from cluster analysis with the average linkage (between groups) method, using a diagonal dissimilarity matrix. The dissimilarity coefficients between pairs of samples were calculated as the relative frequency of significant (at a 5% confidence level) one-way, single-factor, multiple-comparison analyses of variance for the 15 variables considered, using the least significant difference method. **C:** Dendrogram derived from a cluster analysis using the Euclidean distance between sample means of the 15 microwear variables for the 10 groups considered, with the Ward agglomeration method. **D:** Dendrogram derived from a cluster analysis using the Euclidean distance between sample means of the 15 microwear variables for the 10 groups considered, with the complete agglomeration method.

TABLE 6. Discriminant multivariate analysis for the four groups considered[1]

	Variable name	Variable: Entered at step	Variable: Removed at step	Canonical discriminant function coefficients: Standardized Func 1	Standardized Func 2	Standardized Func 3	Unstandardized Func 1	Unstandardized Func 2	Unstandardized Func 3	Correlation coefficient factors/variables: F1	F2	F3
NH	Number of horizontal striations	1		0.85292	−0.40234	0.06717	0.11364	−0.05361	0.00895	0.88↑	−0.04	−0.08
NMD	Number of mesio-occlusal to distocervical striations	2		−0.13922	0.44174	0.73623	−0.03017	0.09573	0.15955	0.09	0.54	0.36↑
STDDM	SD length of disto-occlusal to mesiocervical striations	3		−0.08577	0.36989	0.31878	−0.00169	0.00730	0.00630	−0.17	0.05	0.26
XT	Length of all striations	4		−0.63679	−0.57438	−0.71871	−0.01485	−0.01340	−0.01676	−0.28↓	−0.47↓	−0.03
NDM	Number of disto-occlusal to mesiocervical striations	5	10							0.17	0.50	−0.31
STDT	SD of the length of all striations	6		0.35440	−0.34111	1.38114	0.00958	−0.00922	0.03732	−0.08	−0.25	0.26
STDV	SD of the length of vertical striations	7		−0.21163	0.49627	−0.88303	−0.00468	0.01098	−0.01953	−0.20	0.09	−0.11
XH	Length of horizontal striations	8		0.29812	0.03989	−0.15196	0.00454	0.00061	−0.00231	0.13	−0.35	0.06
NT	Total number of striations	9		0.03694	0.59152	−0.66574	0.00203	0.03253	−0.03661	0.47	0.58↑	−0.27↓
	(constant)						0.06819	−0.42014	1.29517			
NV	Number of vertical striations									0.04	0.47	−0.39
XV	Length of vertical striations									−0.42	−0.16	−0.20
XDM	Length of disto-occlusal to mesiocervical striations									−0.25	−0.11	0.08
XMD	Length of mesio-occlusal to distocervical striations									−0.11	−0.17	0.05
STDH	SD of the length of horizontal striations									0.30	−0.28	0.11
STDMD	SD length of mesio-occlusal to distocervical striations									−0.01	0.04	0.23

[1]The discriminant analysis was performed with a stepwise variable selection method aiming to maximize the minimum Mahalanobis distance (D^2) between-groups selection rule. Minimum tolerance level was 0.001 and prior probability for each group was 0.25. Eight of the 15 variables were finally included in the analysis.
↑ indicates the largest positive correlation for each factor and ↓ indicates the lowest negative correlation of each factor with the variables that entered the analysis.

0.8093 and explains 66.70% of the variance, and factor 2 has a canonical correlation of 0.6581 and explains 26.84% of the total variance. The first factor is highly correlated with the average number of horizontal striations (Pearson correlation coefficient $r = 0.88$), and the second factor is mainly correlated with the number of all the other striations (Table 6) and is negatively correlated with the length of all the striations ($r = -0.47$). Within the discriminant analysis, a between-pair-of-groups multiway ANOVA comparison gave significant results for all the comparisons (carnivorous hunter-gatherers, Hindu, hunter-gatherer from tropical forest, and hunter-gatherer from arid-mesothermal environment). The comparison between the two mixed-diet hunter-gatherers showed the lowest, although highly significant, F statistic ($P < 0.001$). The standardized discriminant function coefficients and the unstandardized function equations obtained are shown in Table 6.

Since the analysis could significantly discriminate between the four dietary groups considered, the discriminant functions obtained were applied to the tooth striation measurements obtained for the fossil sample. Table 7 shows the measurements of the 15 variables considered for the 20 analyzed teeth belonging to Middle and Upper Pleistocene fossil remains. Table 8 shows the classification of each fossil, determined by the discriminant equations shown in Table 6. Figure 2 shows the 95% equiprobable ellipses (Ferembach et al., 1986) of the four dietary groups considered, for the first two discriminant functions obtained, along with the position of each fossil. None of them was classified into the vegetarian Hindu group. Most were included in the modern mixed-diet hunter-gatherer groups (either from tropical or arid environments). Only one fossil (Tabun 1) was clearly classified in the carnivorous group with a 91% probability. Gibraltar 2 was not classified with the discriminant functions obtained because only deciduous teeth were available for this fossil (Table 8). The number of striations in subadult individuals may not be comparable with that of the adult individuals (Pérez-Pérez et al., 1994).

If the fossil remains are grouped into broad phylogenetic groups (archaic *H. sapiens*, Neanderthals, and modern *H. sapiens*), the Neanderthals (specifically Tabun 1, Tabun 2, Amud 1, and La Quina 5) are located either within or close to the 95% confidence region of the carnivorous hunter-gatherer group (Fig. 2.) The Neanderthals from St. Cesaire, Malarnaud, and Marillac are, though, located within the two mixed-diet hunter-gatherers. The anatomically modern *H. sapiens* from Qafzeh and Skhül, and the other modern *H. sapiens* (Cro-Magnon 4, La Madelaine, Abri-Pataud, and Rond-du-Barry) are also located within the mixed-diet modern populations variability range (Fig. 2), with the exception of Veyrier sous Sàleve, which has a large number of mainly vertical striations but a low number of horizontal ones (Table 7). The fossils usually considered as archaic *H. sapiens* (Montmaurin, La Chaise Suard, and La Chaise Burgeois et Delauney) also fall in the mixed-diet range, but have, in general, more striations than the modern hunter-gatherer groups. Broken Hill and Banyoles, though, fall outside the range of the comparative collections (Fig. 2).

Figure 3 shows the dispersion of fossil remains for the NH/NT and NV/NT indexes with respect to the modern hunter-gatherer groups (shown by the 95% confidence interval ellipses). Most of the fossil remains fall between the carnivorous and mixed-diet hunter-gatherers, and all the Neanderthal specimens fall inside the 95% equiprobable ellipse of the carnivorous group. However, only the remains from Amud, Malarnaud, Qafzeh, and Skhül are outside the overlapping region with the mixed-diet hunter-gatherers (Fig 3). Gibraltar 2 falls within the carnivorous range, in the overlapping region with the mixed-diet groups. Although Gibraltar 2 is from a subadult individual, it has been included in the analysis of the indexes for comparative purposes because the relative frequency of striations may be representative of the dietary habits also in the subadult individuals (Lalueza and Pérez-Pérez, 1993). The indexes for Malarnaud are clearly similar to the carnivorous group but the discriminant functions classified it within the mixed-diet groups. Marillac and St. Cesaire are clearly related to the mixed-diet groups with both analysis. Although

TABLE 7. Summary statistics of number, length, and standard deviation of length for the fossil specimens studied[1]

	Variables															Indexes		
	NDM	XDM	STDDM	NH	XH	STDH	NMD	XMD	STDMD	NV	XV	STDV	NT	XT	STDT	NH/NV	NV/NT	NH/NT
Banyoles (ba)	35	154.58	139.10	45	154.29	97.77	16	199.85	166.83	45	195.30	134.27	145	157.70	128.72	1.000	0.310	0.310
Montmaurin (mt)	39	119.13	98.77	13	246.46	188.34	23	118.55	93.09	37	148.45	116.78	112	143.48	123.98	0.351	0.330	0.116
Broken Hill (bh)	37	123.19	105.64	51	76.29	72.66	57	97.94	86.65	58	99.13	78.92	203	97.44	86.50	0.879	0.286	0.251
La Chaise Suard (cs)	19	85.10	29.52	9	214.41	196.96	18	103.53	80.16	15	127.81	59.69	61	120.12	102.75	0.600	0.246	0.148
La Chaise Burgeois (cb)	5	83.05	21.24	21	113.28	72.01	27	109.42	162.63	29	122.66	86.31	82	113.48	113.09	0.724	0.354	0.256
Malarnaud (ml)	11	71.27	31.33	13	80.31	35.76	7	147.61	128.41	37	115.10	81.33	68	104.70	79.01	0.351	0.544	0.191
St. Cesaire (sc)	26	120.54	80.46	14	104.39	51.60	6	110.37	39.21	22	140.49	70.28	68	122.77	70.31	0.636	0.324	0.206
Marillac (mr)	27	226.61	201.42	23	127.36	122.48	17	261.42	246.70	35	245.82	186.46	102	197.67	183.72	0.657	0.343	0.225
La Quina V (q5)	9	229.71	120.64	7	263.22	227.62	26	166.41	82.93	15	203.62	111.03	57	198.08	127.23	0.467	0.263	0.123
Amud 1 (am1)	7	91.28	28.45	6	142.66	88.19	13	145.77	131.65	31	176.76	154.47	57	155.61	136.52	0.194	0.544	0.105
Tabun 1 (tb1)	3	176.24	43.17	3	127.98	95.58	11	147.21	88.97	10	248.95	141.49	27	185.98	114.20	0.300	0.370	0.111
Tabun 2 (tb2)	17	148.32	113.38	3	134.31	96.00	15	158.08	111.43	12	78.97	49.65	47	132.83	104.22	0.250	0.255	0.064
Gibraltar 2 (g2)	24	114.21	69.86	15	117.80	75.79	15	130.00	57.40	39	136.95	120.24	93	126.69	99.25	0.385	0.419	0.161
Skhül 4 (sk4)	16	122.96	74.76	14	103.07	55.60	17	129.15	84.13	44	137.65	91.85	91	128.16	83.69	0.318	0.484	0.154
Qafzeh 9 (qz9)	16	118.36	71.95	9	96.61	20.19	12	100.30	60.23	36	135.45	116.69	73	121.14	93.51	0.250	0.493	0.123
Cro-Magnon 4 (cr4)	28	155.17	84.89	32	132.66	146.68	19	147.19	82.92	44	227.91	182.78	123	174.10	148.07	0.727	0.358	0.260
La Madelaine (md)	18	158.99	122.39	35	156.90	139.76	24	99.52	44.96	23	165.39	88.09	100	145.46	111.71	1.522	0.230	0.350
Rond-du-Barry (rb)	37	117.49	66.15	17	88.74	49.64	9	78.49	30.32	33	205.55	102.73	96	139.01	91.26	0.515	0.344	0.177
Veyrier-sous-Saleve (vs)	8	171.87	219.68	12	124.04	117.10	37	156.99	107.77	53	178.77	125.30	110	164.97	129.52	0.226	0.482	0.109
Abri-Pataud (ap)	26	160.08	78.04	26	109.59	60.32	22	152.06	92.51	65	184.63	116.29	139	160.85	101.32	0.400	0.468	0.187

[1] Names of variables refer to Table 5. Letters in brackets are the symbols used in Figures 2 and 3 for each fossil specimen.

TABLE 8. Discriminant analysis classifications of the fossil materials[1]

	Analyzed tooth			Highest		Second highest	
Fossil (graph symbol)	Jaw	Side	Tooth	Group	Prob.	Group	Prob.
Banyoles (ba)	Mand	Left	M3	Arid	98.13	Tropical	1.68
Montmaurin (mt)	Mand	Right	M1	Tropical	96.61	Arid	3.36
Broken Hill (bh)	Max	Right	M1	Tropical	99.92	Arid	0.08
La Chaise Suard (cs)	Mand	Left	M2	Tropical	95.52	Arid	3.20
La Chaise Burgeois (cb)	Mand	Left	M2	Tropical	98.76	Arid	1.08
Malarnaud (ml)	Mand	Right	M1	Arid	49.82	Tropical	47.17
St. Cesaire (sc)	Mand	Right	M1	Arid	56.38	Tropical	40.05
Marillac (mr)	Mand	Left	M1	Tropical	95.07	Arid	4.74
La Quina V (q5)	Mand	Left	M1	Tropical	95.16	Carnivor.	4.50
Amud 1 (am1)	Mand	Left	M1	Tropical	74.14	Carnivor.	17.74
Tabun 1 (tb1)	Mand	Left	M1	Carnivor.	91.41	Tropical	7.58
Tabun 2 (tb2)	Mand	Left	Pm4	Tropical	91.45	Carnivor.	7.97
Gibraltar 2 (g2)	Mand	Left	m1	Carnivor.	81.91	Tropical	16.25[2]
Skhül 4 (sk4)	Mand	Left	Pm4	Tropical	87.85	Arid	11.58
Qafzeh 9 (qz9)	Mand	Left	M1	Tropical	83.37	Arid	13.87
Cro-Magnon 4 (cr4)	Max	Left	Pm4	Arid	54.54	Tropical	45.37
La Madelaine (md)	Mand	Left	M1	Tropical	88.39	Arid	9.74
Rond-du-Barry (rb)	Max	Right	M1	Arid	65.47	Tropical	33.67
Veyrier-sous-Saleve (vs)	Max	Right	M1	Tropical	99.98	Carnivor.	0.01
Abri-Pataud (ap)	Mand	Left	M1	Tropical	64.12	Arid	35.86

[1]The results shown come from the stepwise discriminant analysis in Table 6. The highest and second highest classification probabilities are percent values derived from the analysis. The probabilities of classification refer to groups arid (hunter-gatherers from arid environment), tropical (hunter-gatherers from tropical environment), and carnivor. (carnivorous hunter-gatherers) as explained in the text. No fossils were classified into the Hindu agriculturalist group.

[2]Gibraltar 2 has been classified with discriminant functions derived from a stepwise analysis done with only 10 variables (discarding the standard deviations of the length due to missing values), of which only eight entered the analysis.

Broken Hill has a large number of striations, the indexes fall within the mixed-diet hunter-gatherer variability. The low number of horizontal striation of Veyrier sous Sàlève is responsible for the similarity of its indexes to the carnivorous group. Finally, only the modern *H. sapiens* from La Madelaine falls within the overlapping region of the mixed-diet groups with the agriculturalists because it has the largest relative frequency of horizontal striations of the fossil remains. With respect to the NH/NV index, the carnivorous groups tend to have low values (Vancouver Islanders, 0.19; Inuit, 0.28; Fueguians, 0.33), due to the major presence of vertical scratches. The more vegetarian groups have higher values of this index (Tasmanians, 0.60; Australians, 0.64; Bushmen, 1.19; andamanese, 1.20; Veddahs, 1.31; Hindus, 2.60). This pattern can also be seen in the fossil remains (Table 7). The Neanderthal specimens have low NH/NV values (carnivorous like) ranging from 0.19 to 0.47, except for St. Cesaire (0.64) and Marillac (0.66), which have values similar to the mixed-diet hunter-gatherer samples. As discussed before, the high index of St. Cesaire might reflect the late dating of the fossil (Vandermeersch, 1984), which would not correspond to a glacial period. However, Marillac, dating back to the Würm II glacial period (Amadei and Navari, 1986), has a considerably high index. The archaic *H. sapiens* tend to have larger values (Table 7), ranging from 0.6 to 1.0, and the modern *H. sapiens* samples vary considerably. The specimens from Skhül and Qafzeh show low values, while the others range from 0.4 to 1.5, with the exception of Veyrier sous Salève, which has a very low value (0.23), similar to those of the carnivorous samples.

DISCUSSION

The factorial analysis of variance shows that, for the studied sample, only the factor of dietary group yields significant differences among the samples considered (Table 5), whereas the factors of sex, tooth, jaw, and tooth side do not seem to affect the buccal tooth striation pattern. The buccal microwear analysis seems to distinguish between the different dietary groups. There is, though, a considerable degree of overlap between the equiprobable ellipses for the first two factors (95% confidence intervals), espe-

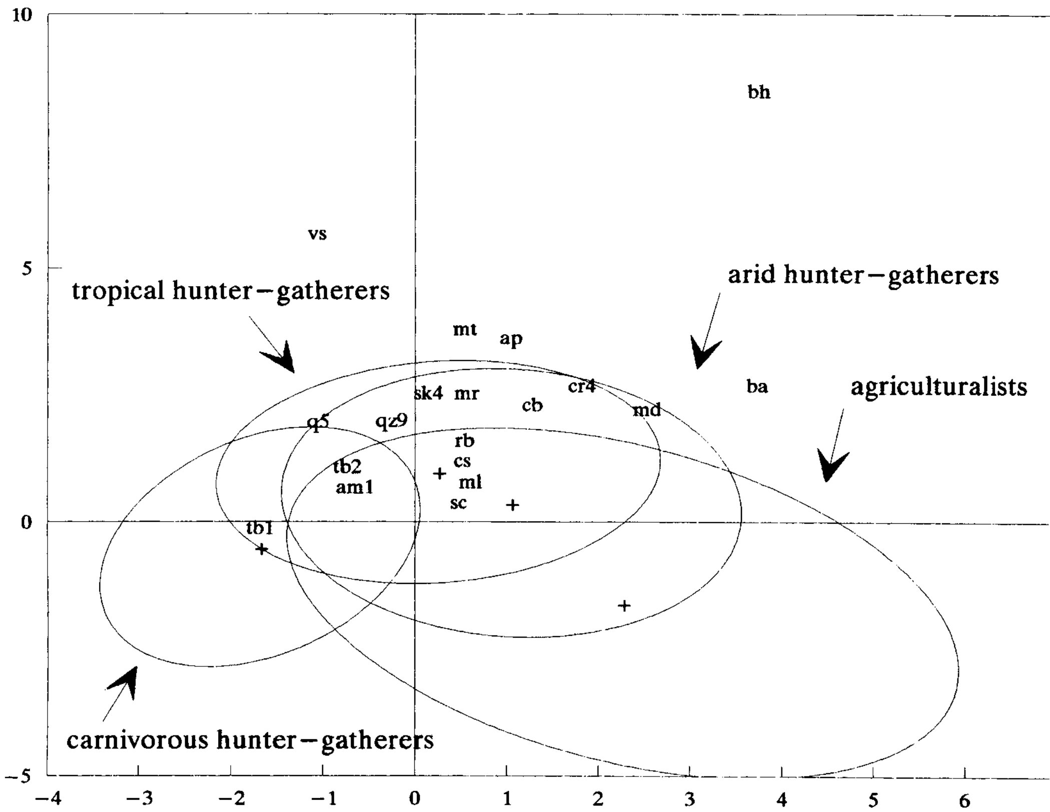

Fig. 2. Multivariate discriminate analysis of the four dietary gorups considered, classifying the human fossil sample. Symbols for fossils are: ba, Banyoles; mt, Mountmaurin; bh, Broken Hill; cs, La Chaise Suard; cb, La Chaise Burgeois; ml, Malarnaud; sc, St. Cesaire; mr, Marillac; q5, La Quina V; am1, Amud 1; tb1, Tabun 1; tb2, Tabun 2; g2, Gibraltar 2; sk4, Skhül 4; qz9, Quafzeh 9; cr4, Cro-Magnon 4; md, La Madelaine; rb, Rond-du-Barry; vs, Veyrier-sous-Sálève; ap, Abri-Pataud. Ellipses represent 95% dispersion of the samples (Ferembach et al., 1986). The + signs are the centroids of the ellipses. The first discriminant factor is plotted on the X axis and the second discriminant factor is plotted on the Y axis.

cially between hunter-gatherers from tropical forests and hunter-gatherers from arid and mesothermal environments. However, the between-pair-of-groups analyses of variance done within the discriminant analysis showed clearly significant differences between the four dietary groups, including the comparison of the two mixed-diet hunter-gatherers. The carnivorous dietary specialization seems to be characterized by a low number of striations, with a high relative frequency of vertical ones. In contrast, the other hunter-gatherer groups have more striations, with a higher proportion of horizontal ones. In the agriculturalist Hindu group this tendency is maximized, having considerably more and longer horizontal than vertical striations.

These general trends in the buccal microwear pattern may be concordant with the suggested relationship between striations and the presence of plant phytoliths in the diet (Baker et al., 1959; Ciochon et al., 1990). A highly vegetarian diet includes more phytoliths than a mainly carnivorous diet, and they may be responsible for the presence of scratches on the enamel surface. However, it is difficult to assess the importance of the phytoliths in the formation of the striation pattern on the buccal surface of teeth. The Inuit, for instance, have an almost negligible vegetable intake in the diet, yet they still

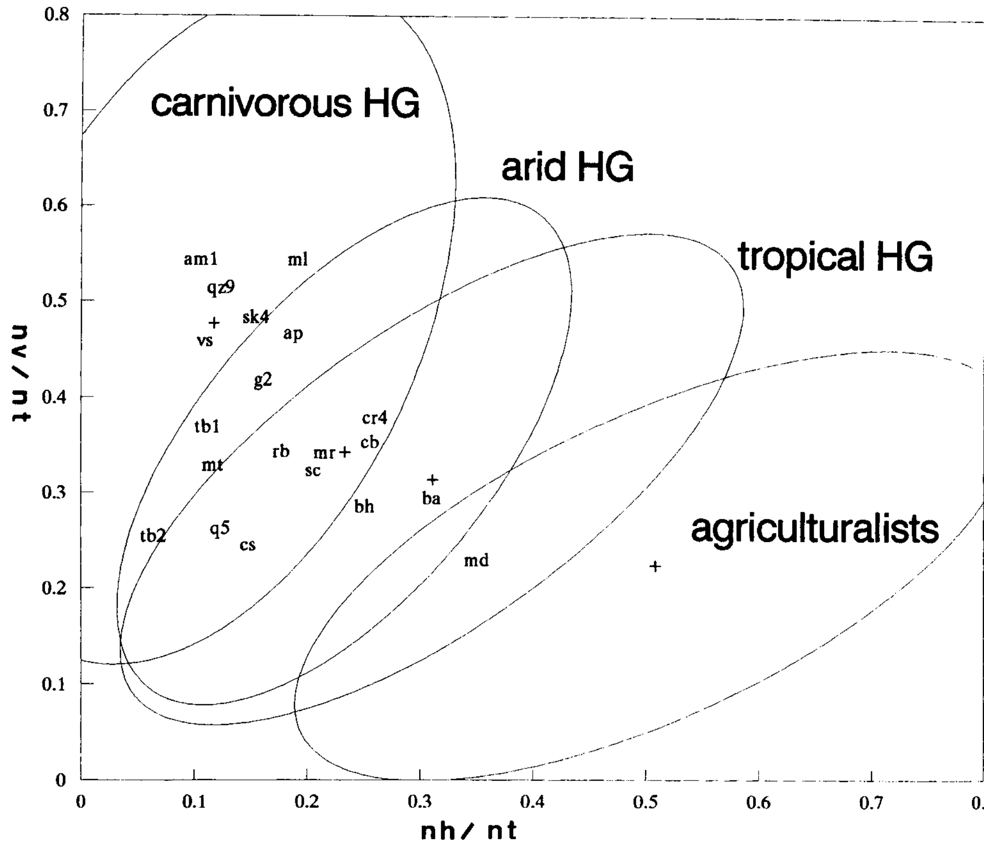

Fig. 3. Plot of NH/NT index vs. NV/NT. Ellipses represent 95% dispersion of the modern dietary groups considered. The + signs are the centroids of the ellipses. Symbols for fossils follow Tables 6 and 7.

have, in our sample, an average density of 39 striations per mm^2 of enamel. This was already observed by Fine and Craig (1981). It is likely that these striations are caused by abrasive particles such as grit, dust, ash, bone powder, or ancient phytoliths from the soil, present in the food. The formation of the striation pattern might then be related, not only to the diet but also to the techniques of cleaning, preservation, and preparation of food materials. Peters (1982) indicates that phytoliths and sand produce striations that are similar in morphology and width (between 0.1 and 1 μm). Maas (1991) also showed that similar-sized abrasives produce similar-sized scratches, and Ungar (1994) has reported a lack of association between striation breadth and orientation. Although the striations caused by the vegetable diet and by exogenous abrasive particles may be morphologically indistinguishable, the high frequency of vertical striations observed in the carnivorous groups may reflect the biomechanics of meat eaters, with predominantly vertical movements of the mandible. In contrast, the mastication of hard and fibrous materials, such as vegetables, may need more horizontal movements (Hinton, 1981; 1982).

From our point of view, the striation pattern, indicated by the number and length of the striations, and by the indexes of striation orientation, reflects different aspects of the dietary habits. The relative frequency of striations might be indicative of the nature of the diet and of the preponderance of plant

and meat food, while the absolute number of striations would be a reflection of the general abrasiveness of the diet. It is clear, though, that both factors (nature and abrasiveness of the diet) may be highly correlated. For instance, in modern hunter-gatherers an increasing number of striations and a higher proportion of horizontal ones may be characteristic of predominantly vegetarian populations.

A different question is whether the tendency found in the microwear of the modern hunter-gatherers can be applied to the fossil specimens. The fossil sample studied consists of isolated remains from a wide range of time periods and geographical areas, with different climates and environments. Most of the fossils analyzed seem to have had a highly abrasive diet, but show similar striation patterns to those of the modern mixed-diet hunter-gatherers (Fig. 2). There exists a considerable degree of heterogeneity in the microwear of these specimens, though, and no clear dietary trend, either temporal or phylogenetic, is present, with the exception, perhaps, of the Neanderthal group. Some of the Neanderthal fossils (Tabun 1, Tabun 2, Amud 1, and La Quina 5) are clearly distributed within or close to the carnivorous hunter-gatherer 95% dispersion range, suggesting that their diet was mainly meat dependent. This might be related to the existence of a subarctic environment in Europe during the Ice Age, which might have favored the development of a predominantly hunting strategy in the Neanderthals. However, the Neanderthal individuals from Marillac, St. Cesaire, and Malarnaud are distributed within the mixed-diet hunter-gatherers. This relatively large dispersion of the Neanderthals' microwear is not surprising, as it may reflect the geographical and temporal diversity of this group. While further analyses of larger samples might help to sort through the variation in the Neanderthal sample, it is interesting to note the position of St. Cesaire. This fossil is morphologically close to the "classic" Mousterian Neanderthals, although the associated industry and the dating (34,000–35,000 B.P., Vandermeersch, 1984; 36,000 ± 2,700 B.P., Mercier et al., 1991) place it at the beginning of the Upper Paleolithic (Vandermeersch, 1984). In the discriminant analysis, St. Cesaire differs from the other "classic" Neanderthals, showing similarities in the microwear pattern with Malarnaud, La Chaise (Suard), and Rond-du-Barry, which probably had a mixed-diet hunter-gatherer strategy. The Neanderthal individual from Marillac also falls within the variability of the mixed-diet hunter-gatherers, and is located close to the modern *H. sapiens* from Skhül and Qafzeh. The archaic *H. sapiens* and the Upper Paleolithic specimens tend to cluster together in the discriminant analysis (Fig. 2), outside the carnivorous dispersion range because of the higher number of striations present in these fossils. The fossil specimens from Banyoles and Broken Hill seem to be detached from the rest of the sample, and this could indicate the existence of dietary specializations in these individuals. In this sense, Broken Hill and Banyoles show several particular traits on their dentition; the unusual degree of dental destruction in Broken Hill (Puech et al., 1980), and the extreme degree of dental wear in Banyoles (Lumley, 1973; Lalueza et al., 1993), with no parallels in the context of the European Pleistocene.

Not any fossil shows a microwear pattern similar to that of the agriculturalist Hindus. Probably, the Neolithic revolution was associated with a considerable shift in the human microwear pattern. Future research should aim toward the analysis of the microwear patterns of populations from the Mesolithic–Neolithic transition, and also to the analysis of more Middle Pleistocene fossils that can help in understanding the inter- and intrapopulational variability of the buccal microwear in human fossils.

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